Chapter 5

Unraveling the components of recruitment limitation in a tropical forest

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Abstract The inability of particular species to regenerate is a potential determinant of the structure and dynamics of plant communities, which frequently explains why local communities are a limited subset of the regional species pool. This recruitment limitation have several components: (i) embryos of a locally present species may not mature into seeds successfully, (ii) the focal community may not receive propagules from a species that occurs in nearby sites, and when they do, (iii) the local biotic and abiotic conditions may not be suitable for successful regeneration. The relative importance of these components as determinants of community structure is rarely assessed, especially in studies involving multiple species. Thus, we report results from a large-scale combined observational and experimental study in the tropical moist forest of Barro Colorado Island in Panama where we attempted to measure the importance of the components of recruitment limitation to explain the absence in the local communities of three regionally common large-seeded tree species (*Dipteryx panamensis*, *Attalea butyracea*, and *Astrocaryum standleyanum*). The relative importance of source and dispersal limitations was assessed by determining the relationships between seeds present in the soil bank and species present in the local community and by seed addition experiments. The importance of establishment limitation was assessed by planting seeds of the species and following their survival from seed predators, and their subsequent germination and seedling establishment success. For all the study species, we found that establishment limitation through post-dispersal seed predation was more important than dispersal limitation. Seeds tended to arrive at most sites, but subsequent seed predation reduced the number of seeds that survived to successful germination by 80%. The subsequent establishment of germinated seeds was generally high in most sites, although conspecific density-dependent mortality (Janzen–Connell-type mechanisms) appeared to limit recruitment in some sites.

Resumen La incapacidad de algunas especies para regenerarse es un determinante potencial de la estructura y dinámica de las comunidades de plantas, que frecuentemente explica por qué las comunidades locales son un subconjunto limitado del pool de especies regional. Esta limitación de reclutamiento tiene varios componentes: i) embriones de la especie presente localmente que no maduan a semilla, ii) la comunidad puede no recibir propágulos de una especie presente en las cercanías, y cuando lo hace, iii) las condiciones bióticas y abióticas locales pueden no ser apropiadas para el crecimiento de las plántulas. La importancia relativa de estos tres componentes como determinantes de la estructura de la comunidad raramente es evaluada, especialmente en estudios que involucren varias especies. Aquí reportamos los resultados de un estudio observacional y experimental a gran escala, en el bosque húmedo tropical de la Isla de Barro Colorado (Panamá), donde intentamos medir la importancia que tienen los componentes de la limitación por reclutamiento al explicarla ausencia en la comunidad local de tres especies de árboles comunes regionalmente. La importancia de la limitación por fuentes o dispersión fue evaluada mediante la determinación de la relación entre semillas presentes en el suelo y las especies presentes en la comunidad local, y mediante experimentos de adición de semillas. La importancia de la limitación de establecimiento fue evaluada plantando semillas de diferentes especies y monitoreando su supervivencia, y su subsecuente germinación y establecimiento de plántulas. Para todas las especies estudiadas, encontramos que la limitación por establecimiento a través de depredación post-dispersión fue más importante que la limitación por dispersión. Las semillas alcanzaron la mayoría de los lugares (probablemente a través de zoocoria), pero la subsecuente depredación reduce el número de semillas sobreviviendo la germinación exitosa en un 80%. El establecimiento de las semillas germinadas a plántulas fue generalmente alto en la mayoría de lugares a pesar de que en algunos sitios la mortalidad dependiente de la densidad (mecanismos Janzen-Connell) aparecieron limitantes.

Introduction

Tropical forests are highly diverse and complex ecosystems. Recent studies have attempted to identify the key processes that cause and maintain their high tree diversity. Some studies have explored how deterministic factors such as environmental filters (*e.g.*, geology, temperature, and topography) explain variation in the species composition at multiple scales (Burton & Bazzaz 1991, Svenning 2001, Bohlman et al. 2008, Jones et al. 2008, Quero et al. 2011), whereas other studies have focused on how stochastic factors such as components of recruitment (*e.g.*, seed dispersal) and asymmetric resource competition determine the community structure (Hurtt & Pacala 1995, Wright et al. 2005). However, studies are needed that quantify the magnitude of these different forces in structuring tropical forest communities. If deterministic processes are more important, there should be a clear match between species requirements and environmental conditions. However, a strong role for stochastic processes may obscure this match. The outcome of this discussion has important conservation consequences, such as the need to protect specific, unique habitats versus the need to protect large areas that would allow stochastic processes to maintain species.

The reasons why a particular species is regionally present but not present in a local community can be separated into three main categories that form a nested hierarchy (Diamond 1975, Zobel et al. 1996, van der Plas et al. 2012). The first broad class of explanations is recruitment limitation, which is also known as regeneration niche limitation (Grubb 1977). The failure of a particular tree species that is present in the regional species pool to make the step in its life history from ovaries and pollen or from vegetative propagules to the successful establishment of a sapling that enters the "competitive arena" with other already established species in a particular local community is an important possible explanation for why a species is absent from a particular community. This recruitment limitation can arise from biotic factors (insufficient animal dispersal vectors or pre- and post-dispersal seed predation), unsuitable abiotic conditions (lack of dispersal by wind or water and seedling desiccation), or a combination of these factors. After a sapling has become established, it may lack the requisite physiological traits to tolerate the prevailing abiotic conditions, such as water logging or high soil pH, which means it fails to be established as an adult plant in the community. In other words, it is limited by its fundamental niche (Hutchinson 1957). Finally, if a species can potentially establish and grow at a site, it may be limited by biotic interactions such as competition for resources with other plants, pathogens, or herbivory, which is also designated as its realized niche limitation (Grace & Wetzel 1981). Thus, recruitment limitation, fundamental niche limitation, and realized niche limitation can all explain the absence of a particular species from a particular community. Of these three types of limitations, recruitment limitation is generally the least understood (Carson & Schnitzer 2008) compared with funda-

mental niche limitation (see reviews in Mulkey et al. 1996, Lambers et al. 2008) or realized niche limitation [see reviews of plant competition (Tilman 1982), plant–herbivore interactions (Crawley 1986, Olff et al. 1999), and plant pathogens (Dobson & Crawley 1994, Wardle 2002)].

The recruitment limitation of tropical forest trees can be subdivided into three potentially limiting steps using the following terminology based on Schupp et al. (2002). First, the ovaries of a plant may not successfully mature into seeds (source limitation) because of selective abortion of embryos resulting from resource scarcity, pollination limitation, or pre-dispersal seed predation (Clark et al. 1998, Crawley 1997, Maron & Crone 2006, Jones & Comita 2010). Second, a local community may not receive propagules from all species in the region (*i.e.*, dispersal limitation), possibly because of the absence of suitable biotic (zoochorous birds, mammals, or bats) or abiotic (wind or water) dispersal vectors (Dalling et al. 2002, Garcia et al. 2005, Forget 1993). Third, when viable seeds reach a site, the local biotic and abiotic conditions may not be suitable for certain species to successfully make the step from an arrived seed to an established sapling (*i.e.*, establishment limitation), possibly because of post-dispersal seed predation (Crawley 1997, Maron & Crone 2006, Jansen et al. 2010), resource competition (Tilman 1997, Paine et al. 2008), herbivory (Muller-Landau et al. 2004; DeMattia et al. 2004, 2006), or pathogens (Mangan et al. 2010, Hersh et al. 2012).

These different recruitment limitation steps are being studied increasingly in tropical forests. Some studies have focused on the roles of seed dispersal, predation, competition, and herbivory in determining species recruitment (Paine & Beck 2007, Terborgh et al. 1993, Augspurger & Kitajima 1992), whereas others have analyzed how species-specific environmental requirements control tree establishment (Ceccon et al. 2003, Huante et al. 1998). Furthermore, some studies have focused on the role of density-dependent natural enemies in controlling recruitment, inspired specifically by the Janzen–Connell hypothesis (*i.e.*, disproportional offspring mortality close to the parents; Janzen 1970, Connell 1978, Mangan et al. 2010).

However, very few studies have simultaneously evaluated the relative importance of two or more of the main types of recruitment limitations in multiple species, *i.e.*, source limitation, dispersal limitation, and establishment limitation. Only Norden et al. (2009) have examined the relative importance of dispersal and establishment limitation using long-term seed-fall data and monitoring seedling plots at a site located within the 82-ha Nouragues Biological station (French Guiana). They showed that seed arrival and habitat conditions affected seedling responses in 14 plant species, but there were also important interspecific differences. They also failed to explicitly include the density dependence of mortality factors (Janzen–Connell effects), although their importance has been demonstrated previously (Maron & Crone 2006). Thus, there is a need for studies that evaluate the relative importance of multiple types of recruitment limitation for multiple species of tropical forest trees.

Thus, we studied the relative importance of seed limitation, dispersal limitation, and establishment limitation simultaneously in three large-seeded tropical forest canopy tree species (*Dipteryx panamensis*, *Attalea butyracea*, and *Astrocaryum standleyanum*) on Barro Colorado Island (BCI), Panama. We did not study source limitation separately. Instead, we inferred its importance on the basis of logical deduction. Studies of seed trapping below trees on BCI suggest that seed production is generally more limiting for tropical trees than seed dispersal (Wright et al. 2005, Muller-Landau et al. 2008; Jones & Comita 2010). We individually mapped the island-wide distributions of the three focal species using a high-resolution georeferenced mosaic of aerial photographs. We used these distribution maps to determine the spatial variation in adult tree density in high detail as a proxy for the potential number of seeds produced locally, and therefore for the degree of local source and dispersal limitations. At 120 sites, we studied the abundance of seeds of the focal tree species in the litter layer. If seeds were absent from the litter layer but present in the local community, this was interpreted as a result of seed limitation. If seeds were absent from the litter layer and the species was absent from the local community, this was interpreted as a result of source limitation and/or dispersal limitation. Establishment limitation was studied in seed addition field experiments at the same 120 sites, where we measured seed predation rates, seed germination, and seedling survival. This allowed us to estimate the relative importance of seed production + dispersal versus establishment limitation, including an analysis of the effects of different environmental properties on establishment (Figure 5.1). We also examined the importance of the initial adult distribution on the actual sapling spatial distribution, which provided a direct test of the patterns predicted by the Janzen–Connell hypothesis at a larger scale than has been studied previously.

Methods

Study site and species

BCI, Panama (9°9'N, 79°51'W), is a 1560-ha tropical moist forest island. The island was isolated from the surrounding mainland between 1910 and 1914 when the Chagres River was dammed to form the central part of the Panama Canal (Leigh 1999). The island has a dry season that starts in December and ends in April or early May. BCI lies at the midpoint of a gradient between the deciduous dry forests of the Pacific Ocean shore, with an annual rainfall of 1800 mm, and the rain forests of the Caribbean side, with an annual rainfall of 3000 mm (Leigh 1999). The forest on the northeast half of BCI is secondary regrowth after widespread cutting and clearing late in the nineteenth century. The other half of the island has received little or no disturbance. The island was declared a reserve in 1923 and has been administrated by the Smithsonian Institution since 1946. The island

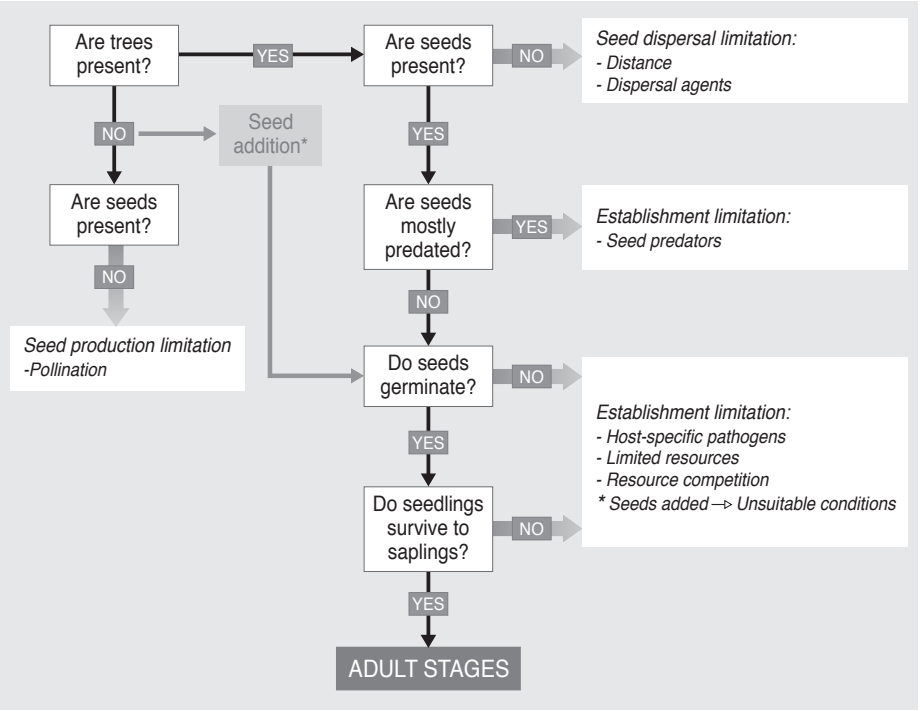

Figure 5.1. Possible observations of early life stage survival in a plot/focal species combination and the type of recruitment limitation that is potentially important for a species in a plot with such conditions. * refers to the processes and limitations observed in the seed addition experiments.

comprises two main geological formations that date from the Oligocene, known as Bohio and Caimito, while the top of the island has a non-sedimentary lithology, *i.e.*, a flow of Andesite lava (Baillie et al. 2007).

We selected three species (*Dipteryx, Attalea*, and *Astrocaryum*), for which we produced island-wide distribution maps (Garzon-Lopez et al. in press). These species are among the most common species on BCI. The species distributions were mapped across the entire island by digitizing the location of canopy-stature individuals in geo-referenced high-resolution aerial photographs. The maps generated were validated against ground data from a 50-ha dynamics plot (Garzon-Lopez et al. 2012). The fruits of these trees are important components of the diets of many generalist mammals and key components in the life cycles of four specialist beetle species (Smythe 1989, Forget 1994, Johnson et al. 1995).

Dipteryx is an emergent tree that grows slowly to reach 40–50 m height with a diameter of 1–1.6 m (Fournier 2003). This species produces approximately 5-cm fruit (Caillaud et al. 2010), which mature between January and April. The fruit is fleshy and has a single seed covered with a hard endocarp. It is dispersed initially

by frugivorous bats and secondarily by scatter-hoarding rodents (Forget & Milleron 1991). Known seed predators include peccaries, squirrels, and great green macaw (Flores 1992).

The arborescent palm *Attalea* reaches 30 m height and 30–60 cm diameter. It produces 1–3 infructescences each year between May and July (Forget 1994). The seeds are dispersed by scatter-hoarding rodents and monkeys and predated by rodents and peccaries. The fleshy fruit contains 1–2 seeds, which are protected by a hard exocarp (Forget 1994). The specialized beetles *Speciomerus giganteus* and *Pachymerus cardo* depend on the florescences and seed to complete their life cycle. The larvae of these beetles drill holes in the exocarp so that they can develop inside while feeding on the endosperm until their development is completed. The larvae then drill an exit hole, which leaves a conspicuous exit mark on the exocarp (Bradford & Smith 1977).

Astrocaryum is a slow-growing palm, which is characterized by long black spines that cover the trunk. It reaches over 20 m height and 30 cm diameter (Pedersen 1994). It produces 3–6 infructescences with 300–800 fruit per infructescence, which mature between March and June when they are dispersed by scatter-hoarding rodents, monkeys, and some birds (Smythe 1989). The fleshy fruit contains a large seed, which is covered by a hard exocarp. The sweet pulp is eaten by a wide variety of mammals (Smythe 1989) including scatter-hoarding rodents that also disperse the seeds. Only a few mammals, such as peccaries (*Tayassu* sp.), predate the seed by cracking open the endocarp. Beetles such as *Pachymerus bactris* and *Coccotrypes* sp. depend on the seeds to complete their life cycle. The larvae of these beetles drill a hole in the endocarp and feed on the endosperm until their development is completed (Johnson et al. 1995).

Experimental design

For the three study species, we estimated the seed/seedling survival at various stages (*i.e.*, dispersal, predation, and germination) of recruitment in 62 sites that varied with respect to the tree density of the focal species. Site selection was based on a range of tree densities from zero to the maximum density found in a plot per focal species.

The tree density was selected as a proxy of seed production and as a measurement of dispersal limitation (available seeds/seed sources). Initially, it was estimated from distribution maps of the tree species, which were produced from high-resolution aerial photographs (Garzon-Lopez et al. 2012). The high and low seed production areas for each species were determined by placing a 1-ha grid over the island and estimating the number of individuals per grid. Using this density map, grids were selected within the 0–25% (low density) and 75–100% (high density) tree density percentiles. A total of 20 sites (each site, 1 ha) were selected for each density range, which resulted in 40 sites per species. Whenever possible, the same site was used for various species (22 sites of two species and 15 sites of three

species); therefore, 62 sites were surveyed across the entire island. At each site, we measured the adult density (from the ground), seed density, seed predation rates, seed germination, and seedling predation as follows.

(1) ADULT DENSITY: The parent tree density was determined by ground surveys, which recorded the GPS positions of all adults of the tree species studied. These provided a measurement of the seed source density for each species evaluated.

(2) SEED DENSITY AND PREDATION: Endocarps were collected at 10 points, which were selected randomly in each 1-ha plot. We placed a 1 m^2 quadrat at each surveyed point and searched for all of the endocarps in the soil up to a depth of 5 cm. To determine predation events, all of the endocarps were examined by recording their predation status (*i.e.*, predated or intact) and the type of predator (*i.e.*, bruchids, rodents, or scolyotids) on the basis of scars left on the endocarps (Silvius 2002; Chapter 4).

(3) SEED GERMINATION AND SEEDLING PREDATION: A seed addition experiment was conducted at the centre of each site by establishing a 5 m^2 germination plot where each seed was protected with an iron mesh to prevent seed predation. We buried 25 seeds in each of these plots. Germination and predation were recorded 2, 12, and 24 months after seed addition.

Data analysis

Using the data collected, we estimated seed arrival and survival (determined by source and dispersal limitations) and seed germination and seedling establishment (controlled by establishment limitation). We calculated the percentage of seeds at each life stage (*i.e.*, dispersed seeds, seeds escaping predation, seed germination, and 1-year seedling establishment). Based on the results, we estimated the percentage where each type of limitation (dispersal/source or establishment) determined the species distribution. The percentages of seed/seedling survival during each life stage were compared using the nonparametric Wilcoxon signed-rank test.

We explored the effects of the density of parents and the predation rates at each site on seed survival and further recruitment. To achieve this, we examined whether the parent density was related to seed recruitment. We also evaluated how the forest structure and dynamics (summarized as forest age in the analysis) might affect density versus recruitment (Svenning et al. 2004). These analyses were performed using a mixed model Poisson regression where seedling density was the response variable, tree density and soil were the predictor variables, and forest age was included as a random effect in the model (which affected the intercept and slope). Second, on the basis of the actual number of seeds available for recruitment at each site, we subtracted the seeds predated from the total number of seeds found at each site to estimate dispersal limitation in terms of source limitation. This factor was high and it varied among sites; therefore, we only evaluated its effect on dispersal limitation at the scale of the entire island.

Results

A total of 769 adults of the study species were censused in the field, and their densities ranged between 0 and a maximum of 56 individual adult trees/ha for *Astrocaryum*, 39 trees/ha for *Attalea*, and 8 trees/ha for *Dipteryx*. A total of 5790 endocarps of the three species were collected from all sites, and their densities ranged from 0 to a maximum of 139 endocarps/ha for *Astrocaryum*, 196 endocarps/ha for *Attalea*, and 219 endocarps/ha for *Dipteryx*. Of the 25 seeds per species per 5 m^2 added to each site, 10% (SE = 2.1) of *Astrocaryum*, 28% (SE = 4.1) of *Attalea*, and 34.7% (SE = 4.1) of *Dipteryx* germinated (Figure 5.2).

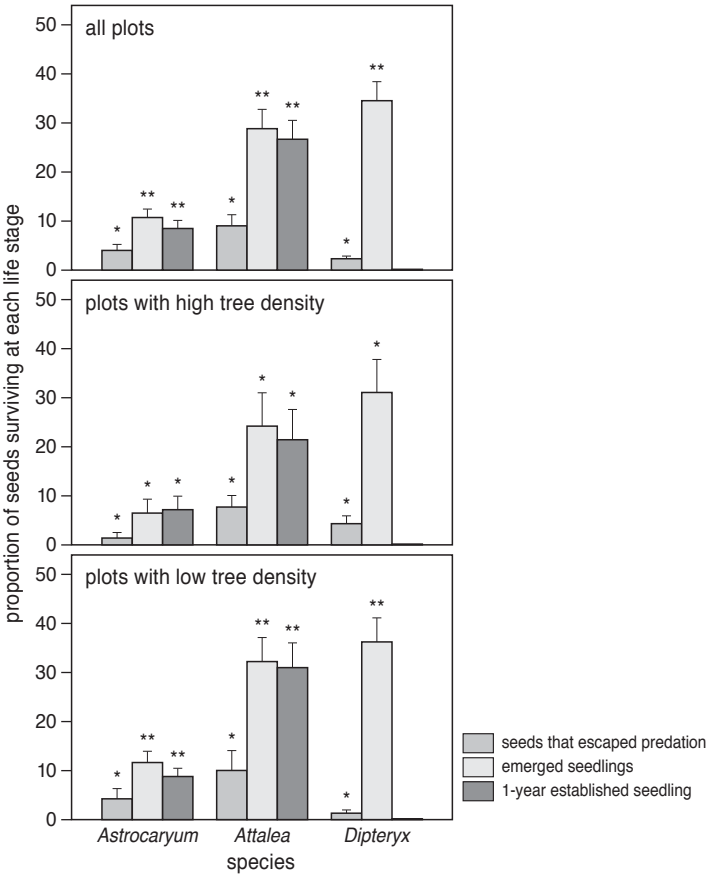

Figure 5.2. Variation in seed density during each stage of establishment limitation (seeds that escapes predation, emerged seedlings, and 1-year established seedlings) in all plots and specifically in plots with high tree densities and those with low tree densities. The y-axis shows the percentage of seeds from each species per stage. The whiskers corresponds to the 95% standard error around the association estimates. The results of the Wilcoxon tests are also presented. Significant differences among life stages within species are marked with *, where * and ** are significantly different.

Source/dispersal limitation

In general, source limitation appeared to be high in all species, with low average densities of trees per plot. The average tree densities per 1-ha plot were 3.2 for *Astrocaryum*, 8.3 for *Attalea*, and 0.4 for *Dipteryx*.

Limitation *via* dispersal was low. In the 40 plots surveyed, 77% of the plots had at least one *Attalea* seed, 96.6% of the plots had at least one *Astrocaryum* seed, and 82% had at least one *Dipteryx* seed (Table 5.1). However, the average number of seeds, even in the plots with high adult tree densities (average number of trees: *Attalea* = 15.4, *Astrocaryum* = 8.7, and *Dipteryx* = 1.6; Table 5.1), was 60–80 seeds per species, which was 10 times lower than the average production of a single tree.

Establishment limitation

Seed predation reduced the number of seeds available for further stages by 96.7% (SE = 1.55) for *Astrocaryum*, 92.5% (SE = 2.31) for *Attalea*, and 97.7% (SE = 0.72) for *Dipteryx*. Seed predation was only higher with high tree densities in case of *Dipteryx* because 1.2% of seeds escaped predation at high tree densities, whereas 4.5% of seeds escaped predation at low tree densities (Table 5.1). Using the nonparametric Wilcoxon test to compare the percentage of seed survival during

Table 5.1. Dispersal limitation (seed source counts and seeds in the soil bank) and establishment limitation (% seeds that escaped predation, germinated and established) for all plots, high density plots, and low density plots per species.

Tree species	Dispersal limitation		Establishment limitation		
	Total number of seed sources per 1-ha plot (adult trees)	Total number of seeds found per 1-ha plot	% seeds escaped predation	% seeds germinated	% seedlings 1- year established
All plots					
Astrocaryum	3,2 (0,63)	26,9 (5,2)	3,9 (1,5)	10,5 (2,1)	8,5 (1,6)
Attalea	8,3 (2,1)	48,5 (11,3)	9,1 (2,3)	28,6 (4,1)	26,8 (3,9)
Dipteryx	0,4 (0,2)	41,6 (13,1)	2,1 (0,7)	34,7 (4,1)	0
Low tree density plots					
Astrocaryum	1,86 (0,4)	18,2 (2,9)	4,4 (1,9)	11,5 (2,6)	8,9 (1,9)
Attalea	2,5 (0,6)	35,1 (15,3)	10,3 (3,7)	32,4 (4,8)	31,2 (4,8)
Dipteryx	0	24,1 (9,7)	1,2 (0,7)	36 (5,2)	0
High tree density plots					
Astrocaryum	8,7 (0,9)	60 (17,8)	1,6 (1,0)	6,7 (2,8)	7,3 (2,8)
Attalea	15,4 (3,2)	64,9 (16,1)	7,6 (2,6)	24 (7,0)	21,3 (6,1)
Dipteryx	1,6 (0,4)	87,2 (34,4)	4,5 (1,6)	31,2 (6,6)	0

each stage of establishment limitation (post-dispersal predation, seed germination, and 1-year seedling establishment) in all plots, we found that seed survival in the post-dispersal seed predation stage was significantly lower than that in the other two stages of establishment limitation for all species. The same pattern was observed when we compared only plots with low tree density, whereas no significant differences in seed survival were observed among stages for any of the species with high tree densities.

Discussion

In this study, we showed that despite the clustered distribution of seed sources (adult trees) on BCI (Garzon-Lopez et al. 2012), low dispersal limitation allowed the seeds of the species evaluated to reach locations far from the source trees and they were present in most areas on BCI, although source limitation was high. Seed predation (the evaluated component of establishment limitation) had a strong effect on seed survival by reducing the amount of seeds available for germination. In addition, seed germination appeared to be high during early seedling recruitment; therefore, site suitability depended on soil properties and local conditions (*e.g.*, the adult tree densities and seedling predators). Janzen–Connell-type mechanisms have the potential to turn the site from suitable (based on abiotic conditions) to unsuitable, thereby making seed dispersal irrelevant for determining establishment limitation. Overall, these results suggest the importance of the spatial arrangement of adult trees for species recruitment.

Of the various seed predators of *Attalea*, *Astrocaryum*, and *Dipteryx*, some act as seed dispersers (*e.g.*, mammals) moving the seeds great distances from the parent trees (Galvez et al. 2009). In our study, the seeds of all species were present in 80% of the sites but only 40% of the sites had adult trees of all species (85% *Astrocaryum*, 40% *Dipteryx*, and 67% *Attalea*.). Thus, the spatial distribution of seeds may have been controlled by dispersal (*e.g.*, seeds were found in areas with no adult trees), which could potentially be a critical factor that allows seeds to reach areas with low adult densities. This agrees with previous studies, which have shown the importance of seed dispersal for reaching available sites (Nathan & Muller-Landau 2000, Clark et al. 2007) at fine scales. The large scale of our survey indicated reduced dispersal limitation, which demonstrates the limited importance of dispersal for determining the community composition of a site.

Seed predation is also believed to be an important filter for establishment limitation (Turnbull et al. 2000). This was confirmed in our study because it was the most important filter that determined the observed distribution of parents with viable seeds (>80% of dispersed seeds were predated and failed to germinate). Seed predation was an important cause of seed mortality; therefore, it may be a critical limiting factor that shapes the spatial distribution and subsequent establishment

rates for viable seeds. Seed predation is a spatial process that depends on the spatial distribution of predators, which depends on the spatial arrangement of their food, shelter, and predators (Brown 1999, Mayor et al. 2009). Therefore, seed predation is a dynamic component that limits species recruitment and that might only be surpassed in importance by dispersal, particularly in cases where seed production is sufficiently high to match seed predation rates (Crawley 2000, Orrock et al. 2006).

After the seed spatial distribution matrix is set (*i.e.*, the sites that have seeds and those that do not), the site conditions control the fate of the seed (germination, remaining in the soil bank for secondary dispersal, or termination by predators/pathogens). Only after overcoming the dispersal filter, does establishment limitation become an important factor that shapes the spatial distribution of seedlings. In our study, at least one seedling germinated at each site; therefore, establishment limitation *via* seed germination was low.

The pathogen and predator density is hypothesized to be higher close to the parent trees (Janzen 1970, Connell 1978). This was observed in our study where the tree density had a negative effect on germination. Specifically, sites were most suitable for germination when the tree density was low and less suitable when the tree density increased. This suggests a spatial tradeoff between survival and germination rates where past suitable sites (high tree recruitment and high tree density) become sites with high establishment limitations because of density-dependent competition (high seed density), in addition to the presence/accumulation of pathogens and predators (Augspurger 1984). However, unsuitable sites have the potential to become suitable because of high seed mortality, which may occur *via* a reduction in density-dependent competition. This could enhance the recruitment opportunities of surviving species, even in high tree density conditions. In *Dipteryx*, seedling predation was extreme and no seedlings were found alive six months after the initial survey. This strong seedling predation pattern and high seed germination were previously reported on BCI by De Steven & Putz (1984), which were attributed to the abundant mammal populations on the island. A general finding was that each species responded differently to the site conditions, suggesting that species-specific requirements and density-dependent processes have specific effects that depend on the autoecology of each species.

Negative density dependency was previously shown to control recruitment by studying the effect of seed density on further recruitment (Harms et al. 2000, Wright et al. 2005). In our study, there was a correlation between tree density and recruitment for two of the three species (*Attalea* and *Astrocaryum*), but the effects of recruitment differed in strength at each site depending on the local conditions (abiotic factors and predation rates). This suggests that there is a tradeoff between abiotic and biotic conditions at the community level, which results in varying species recruitment depending on the spatial and temporal context. This might be an important control on species coexistence in the tropical forest.

The possibility of studying forest dynamics at a relevant community scale provides a new perspective that aids the understanding of the forest structure and dynamics by studying a single species in a measurable context at a larger scale than ever before. Special attention should be paid to the effect of seed predation on species recruitment because an imbalance in this factor caused by poaching and changes in the food web (Wright & Duber 2001) might result in a damaging shift in the species composition and biodiversity maintenance.

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